

Secondary olfactory connexions and the anterior commissure in the coypu, *Myocastor coypus*

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In a number of mammals it has recently been shown that the distribution of secondary olfactory fibres within the hemisphere is more limited than previously thought, and that few, if any, enter the anterior limb of the anterior commissure. Important work on these lines is that of Lohman (1963) in the guinea-pig and of Powell, Cowan & Raisman (1965) in the rat. These authors, using the Nauta technique, were unable to trace degenerated fibres from lesions confined to the olfactory bulb either to the anterior commissure or to the deeper amygdaloid nuclei such as the central nucleus and the bed nucleus of the stria terminalis.

Connexions to these amygdaloid nuclei and fibres running in the anterior commissure have been described by previous authors (e.g. Clark & Meyer, 1947; Adey, 1953; Allison, 1953*a*), and were accepted by Allison in his review of the central olfactory apparatus (1953*b*). These findings were based chiefly on the use of the Glee's silver technique which has been shown sometimes to give false positive results (Cowan & Powell, 1956), but both Lohman (1963) and Powell *et al.* (1965) have given full and critical discussions of the previous work which it is unnecessary to repeat here. The purpose of the present paper is to place on record some similar observations in another mammal, *Myocastor coypus*. They are based on the use of the Nauta technique in specimens with lesions in the olfactory bulbs, in the anterior olfactory nucleus and in the anterior commissure close to the median plane.

MATERIALS AND METHODS

Twenty-one coypus were used. Their weights ranged from 1.60 to 6.75 kg, so that all were young, probably between 3 and 9 months of age. Both males and females were used without distinction. They had all been caught in the wild and appeared healthy, and no sign of ill-health developed during the period of the experiments.

All operations were performed under ether anaesthesia with full aseptic precautions. After opening the skull and incising the dura mater the lesions were made with an iridectomy knife, meibomian cyst scoop, thermo-cautery, or by suction, and they fall into three groups:

(i) lesions confined to the olfactory and accessory olfactory bulbs: eight specimens;

(ii) lesions involving the olfactory peduncle and anterior olfactory nucleus: eight specimens;

(iii) lesions of the anterior commissure without damage to the anterior olfactory nuclei or olfactory bulbs: five specimens.

Survival times varied considerably but most of the specimens fell into two groups with survival times between 10 and 14 d (seven specimens) or between 20 and 28 d (eleven specimens). The group with the longer survival time seemed to give slightly more definite staining of degeneration products, possibly due to more complete degeneration in the tracts affected, and probably about 21 d is the optimum period for the Nauta technique in this animal. The one 7 d specimen showed definitely less evidence of degeneration than in specimens with a similar lesion but longer survival. Two specimens with survival times of 43 and 56 d respectively show satisfactory evidence of degeneration in situations such as the lateral olfactory tract but are not reliable for the study of preterminal degeneration.

The Marchi technique was used as well as the Nauta in two specimens but gave no additional information, and, as expected, was less satisfactory than the Nauta technique for tracing the fine preterminal ramifications of fibres. The results to be reported are therefore based entirely on the use of Nauta stained frozen sections (Nauta & Gyax, 1954). The characteristics of the method and the criteria used for judging degeneration do not differ significantly from those previously described for the coypu (Goldby & Kacker, 1963), but in the present study the possibility that some of the degeneration demonstrated is retrograde rather than antegrade must be considered.

Powell & Cowan (1964) have pointed out that the assumption that antegrade can be distinguished from retrograde degeneration because the latter takes longer to become demonstrable, is not always valid. These authors and others have demonstrated retrograde degeneration in thalamic nuclei of the rabbit, using the Nauta technique, after survival periods of 10 d and even less (8 d, Cragg, 1962). It does not necessarily follow that retrograde degeneration in the basal rhinencephalic structures of the coypu appear as rapidly or even at all, but one cannot assume that this is so, particularly as in many of the present experiments the survival periods have been longer than those usually employed. In spite of this, the degeneration has been reported as antegrade for two main reasons.

First, the fine granularity, lacking a pericellular arrangement and related to the break up of cell bodies and dendrites, which Powell & Cowan found to be characteristic of retrograde degeneration in the thalamus, has not been observed in any of the situations studied; and secondly, after complete section in the median plane of the anterior commissure, which presumably contains fibres running in each direction in equal numbers, many fibres retain a normal appearance on both sides of the lesion, in one case after a survival period of 43 d. Unless one makes the unlikely assumption that retrograde changes become demonstrable earlier than antegrade, the degeneration seen in this situation must all be antegrade. It appears therefore that demonstrable retrograde degeneration in the structures relevant to the present study develops much more slowly, and perhaps not at all, in the coypu, and this is the assumption on which the findings are reported.

In addition to the experimental material several series of sections stained by routine methods (Nissl and Weigert) were available for the study of the normal features of the olfactory bulbs and basal parts of the rhinencephalon. The results of

this study will be reported elsewhere; here it need only be said that the regions studied showed no important difference from the same regions in comparable mammals such as the rat.

Degeneration after lesions confined to an olfactory bulb

Eight specimens are available in two of which the accessory as well as the main bulb is involved in the lesion. All are very similar and specimen 171 (15 d survival) may be taken as an example.

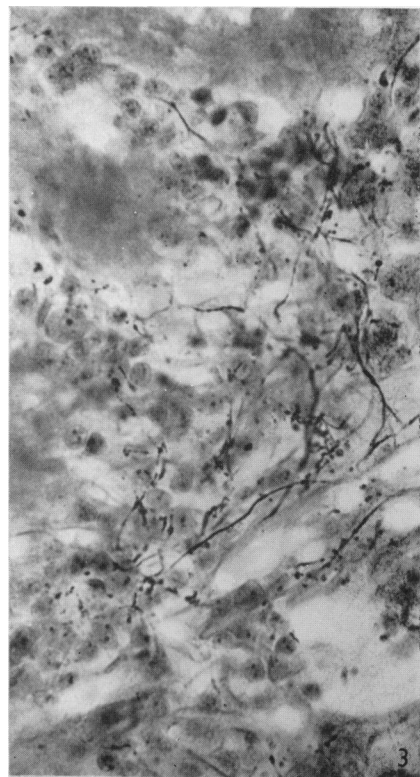
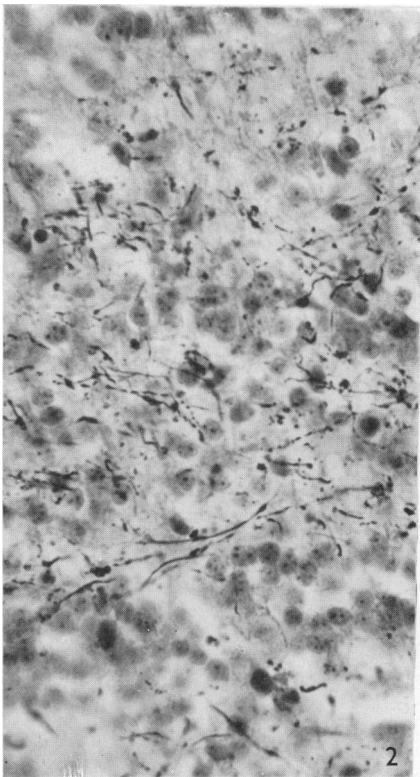
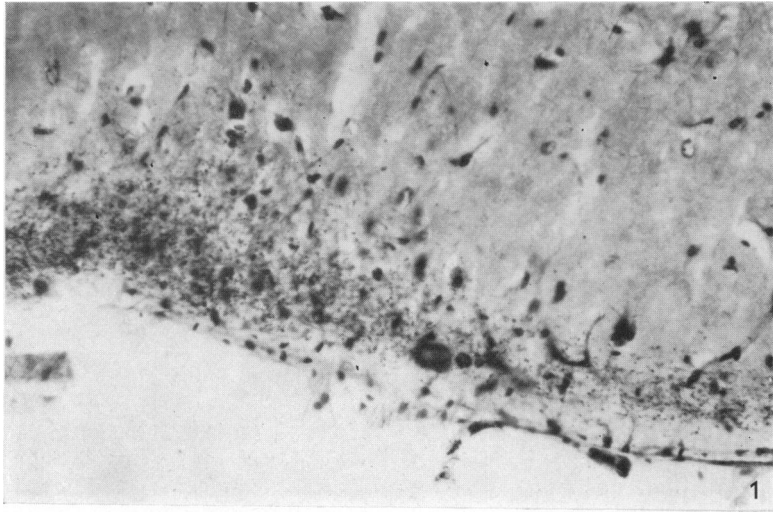
In this specimen the lesion is fairly small being limited to the antero-dorsal part of the main olfactory bulb. Degeneration in the olfactory peduncle is heaviest over the lateral aspect of the anterior olfactory nucleus but extends also to the ventral and, to a less extent, the dorsal aspect where some may be preterminal. Most of it is quite superficial in the outer part of the molecular layer of the nucleus. The degeneration can be traced caudally to extend over the whole of the piriform cortex to the bottom of the rhinal fissure (where it ends abruptly) and medially over about the antero-lateral third of the olfactory tubercle. It does not extend to the entorhinal or posterior piriform cortex. Level with the caudal border of the olfactory tubercle an ill-defined superficial collection of cells represents the nucleus of the lateral olfactory tract. Degeneration is present superficial to these cells and there is some evidence of a slight medial spread into the region of the diagonal band and its nucleus, but the latter is not clearly separable from the nucleus of the lateral olfactory tract. Further caudally the degenerated fibres run along the amygdaloid fissure and the border of the cortical amygdaloid nucleus in small numbers (Fig. 1). It should be emphasized that all the degeneration is quite superficial and in the outer part of the molecular layer. No degeneration is present in the anterior limb of the anterior commissure and none in the deeper parts of the amygdala or indeed, in any other part of the hemisphere.

The findings are almost identical in the other seven specimens in several of which the bulbar lesions are considerably larger. In some (e.g. specimens 172 and M 12) an occasional fragmented fibre can be seen in the anterior limb of the anterior commissure but the difference from normal control specimens is so slight that it cannot be considered significant. In all of them the amount of degeneration which reaches as far caudally as the amygdala is small but in several it spreads beyond the region of the amygdaloid fissure into the molecular layer over the cortical amygdaloid nucleus but not to any other of the amygdaloid nuclei.

In two specimens, M6 and M7, the accessory olfactory bulb had been wholly or partly destroyed as well as much of the main bulb but no evidence was obtained suggesting that its connexions differ from those of the main bulb. It is possible of course that they are more limited in their distribution within the same field, but attempts to produce lesions confined to the accessory bulb were unsuccessful and no more can be said.

Lesions of the olfactory peduncle and anterior olfactory nucleus

In six specimens the lesion is in the olfactory peduncle (with or without associated damage to the olfactory bulb) and in all of them fibres passing caudally from the bulb have been divided, in most cases completely. In two further specimens almost complete destruction of the bulbs is associated with damage only to the rostral extremity of the anterior olfactory nucleus.



As expected, all specimens show degeneration in the situations where it is found after bulbar lesions alone and in this respect there is little difference from those already described. Two show a rather more extensive spread of degeneration into the molecular layer of the cortical amygdaloid nucleus, but the specimens are not uniform in this respect and variations seem to bear no relation to the extent of involvement of the anterior olfactory nucleus. Three show what appears to be preterminal degeneration close to the perikarya of pyramidal cells in the piriform cortex and the cortico-amygdaloid transition area. After lesions limited to the bulb, degeneration is seen only in the molecular layer so that the fibres which end more deeply have probably degenerated as a result of the lesion in the anterior olfactory nucleus and presumably arose there. As before, no degeneration is present in the deeper amygdaloid nuclei such as the central nucleus or the bed nucleus of the stria terminalis.

In all these specimens however there is definite degeneration in the anterior limb of the anterior commissure. This is well shown in specimen M4 (Fig. 4) where the peduncle is completely destroyed on one side. There is also some damage to the frontal pole of the hemisphere, as there is in most of the specimens with peduncular lesions. This has led to degeneration in the corpus callosum and in fibre bundles passing through the corpus striatum to the internal capsule which is irrelevant to the present study and will not be referred to again.

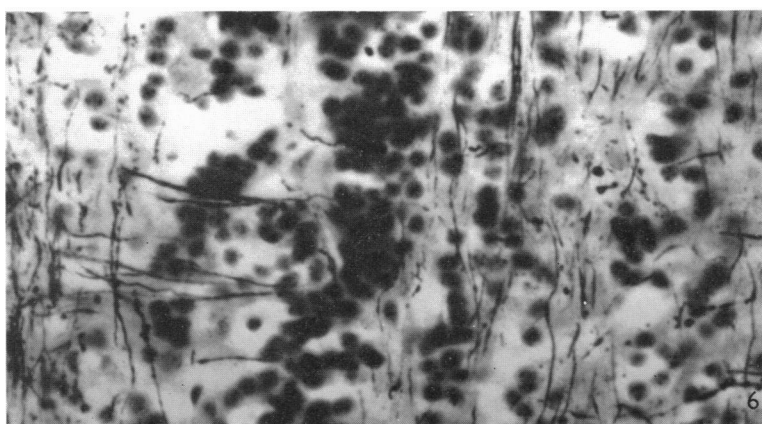
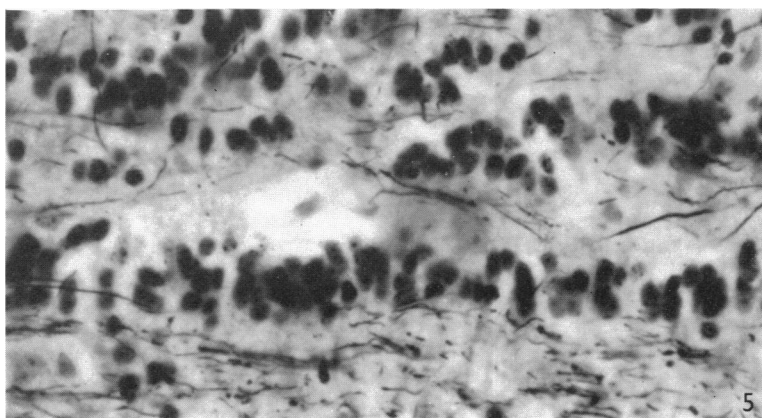
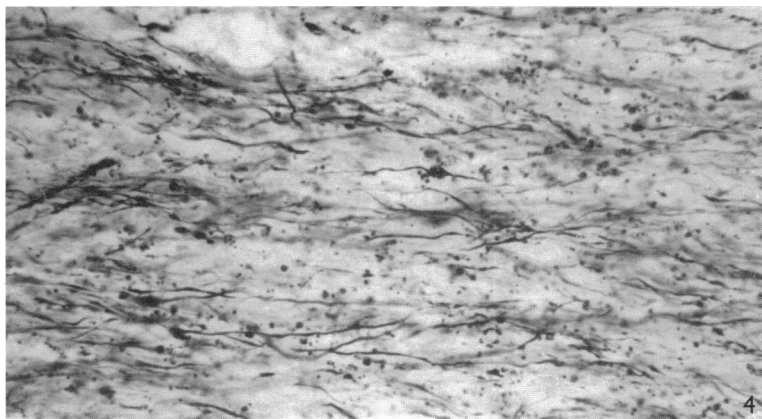
In another specimen (M9) the peduncle is severed close to its attachment to the hemisphere, destroying the caudal part of the anterior olfactory nucleus and dividing both the lateral olfactory tract and anterior limb of the commissure, but with little other damage. On the operated side degenerated fibres can be followed rostrally in the core of the remaining part of the peduncle to the inner granular layer of both main and accessory olfactory bulbs and some can be traced into the outer plexiform and the glomerular layers, where they ramify among the periglomerular cells. These must be bulbo-petal fibres, running mainly through the anterior limb of the commissure, but there is some degeneration in the deeper part of the lateral olfactory tract which could provide an alternative pathway. It is obvious that the bulbo-petal fibres could come either from the part of the anterior olfactory nucleus which has been destroyed by the lesion, from some part of the ipsilateral hemisphere caudal to the lesion, or from the opposite hemisphere through the anterior commissure.

Caudal to the lesion degenerated fibres can be traced through the anterior commissure to the peduncle and olfactory bulb of the opposite hemisphere. Here some of them end in the inner granular layer and although an occasional fragmented fibre can be seen in the outer plexiform layer there are none among the glomeruli and the periglomerular cells. These crossed fibres must have arisen in the damaged anterior

Fig. 1. Preterminal degeneration in the superficial part of the molecular layer in the amygdaloid fissure (on the left in the photograph) spreading to the right along the rostral border of the cortical amygdaloid nucleus. Specimen 171 with a lesion confined to the olfactory bulb; $\times 175$.

Fig. 2. Degeneration in the inner granular layer of the olfactory bulb after a lesion in the ipsilateral anterior olfactory nucleus. Specimen M2, $\times 420$.

Fig. 3. Degeneration among the periglomerular cells in the same olfactory bulb as that shown in Fig. 2. $\times 420$.



olfactory nucleus because they are not seen after lesions confined to the opposite bulb.

The fact that it is only on the operated side that degenerated fibres extend to the glomerular layer of the bulb suggests that there are at least two sets of bulbo-petal fibres: (i) the fibres which cross in the anterior commissure from the opposite anterior olfactory nucleus, the great majority of which end in the inner granular layer; and (ii) the fibres which run to the periglomerular cells and are demonstrated only on the operated side. The latter could be crossed or uncrossed, but assuming that the degeneration is antegrade, must have arisen caudal to the anterior olfactory nucleus and could have run either in the anterior limb of the commissure or in the deeper part of the lateral olfactory tract. The presumption is that they run in the deeper part of the lateral olfactory tract which is degenerated only on the operated side, and if so they are probably uncrossed fibres.

In the specimen M4 with a larger peduncular lesion, both right and left bulbs can also be compared. The findings are very similar, although an occasional fragmented fibre is seen among the periglomerular cells on the side opposite to the lesion and degeneration among the granular cells is less marked. On the operated side the degeneration among the periglomerular cells is very prominent. In specimen M2, also with a peduncular lesion, the degeneration in the inner granular layer and extending to the periglomerular cells on the ipsilateral side is particularly marked (Figs. 2 and 3). In two other specimens (M8 and M15) only the bulb contralateral to the lesion could be examined and neither show clear degeneration among the periglomerular cells although it is present in the inner granular layer (Fig. 5). Satisfactory sections were not obtained from the olfactory bulbs in the remaining three specimens, in two of which the anterior olfactory nucleus is damaged only slightly at its rostral extremity. In both of these there is very little degeneration in the anterior limb of the commissure.

In addition to the terminations in the olfactory bulbs, in three specimens (M4, M15 and M8) there appears to be some preterminal degeneration among the cells of the contralateral anterior olfactory nucleus, chiefly in the pars dorsalis and the pars externa. The appearance is not very definite, however; it is not confirmed by the other specimens and it is difficult to convince oneself that the degeneration is not in fibres of passage which run to the bulb. In view of the observations made in other mammals (e.g. by Lohman, 1963, in the guinea-pig), it is very probable that the anterior limb of the anterior commissure does carry fibres to the anterior olfactory nucleus in the coypu, but the present evidence is not conclusive.

Fig. 4. Degeneration in the anterior limb of the anterior commissure as it crosses the median plane after a lesion in one anterior olfactory nucleus. Note the presence of some heavily impregnated normal fibres. Specimen M4, $\times 420$.

Fig. 5. Degeneration in the inner granular layer of the olfactory bulb after a lesion of the opposite bulb and anterior olfactory nucleus. The degeneration is light because only about the rostral third of the latter is destroyed. Specimen M15, $\times 440$.

Fig. 6. Degeneration in the inner granular layer of an olfactory bulb after section of the anterior commissure in the median plane. The degeneration is heavy because all the fibres from the contralateral anterior olfactory nucleus have been divided. Specimen M14, $\times 440$.

In normal material the anterior limb of the anterior commissure is seen to be joined by a few small fibre bundles which appear to come from or go to the basal surface of the brain in the region of the olfactory tubercle and the adjacent piriform cortex. In three of the experimental animals (M2, M4 and M9) these bundles are completely degenerated on the operated side and slightly contralaterally. They pass towards a region deep to the rostral part of the piriform cortex and olfactory tubercle where some diffuse degeneration debris can be seen. They may also account for the pre-terminal degeneration close to perikarya in the piriform cortex already noted. In one of the specimens (M4) a few of the degenerated fibres enter the medial fore-brain bundle and can be traced to the lateral part of the hypothalamus, but the lesion in this specimen is large and may involve the anterior border of the olfactory tubercle. The fibre bundles in question probably come from the anterior olfactory nucleus and end in basal rhinencephalic structures, mainly ipsilaterally, and possibly to a small extent contralaterally. The specimens in which these observations were made all had extensive lesions in the anterior olfactory nucleus with complete or almost complete transection of the peduncle, close to its junction with the hemisphere. In the other four specimens the lesions were mainly in the rostral part of the anterior olfactory nucleus. This may account for the lack of degeneration so far as the bundles in question are concerned, but further confirmation is desirable.

Lesions of the anterior commissure

Attempts were made in five specimens to cut the anterior commissure in the median plane. This was done by inserting a narrow knife blade vertically in or close to the median plane to a depth of 15 mm, a distance which carried the point a little ventral to the level of the commissure. The fronto-parietal suture in the skull marks the position of the commissure in the rostro-caudal direction and a cut was made for 2 or 3 mm both rostral and caudal to the line of the suture. As expected, this operation caused much associated damage to such structures as the corpus callosum, hippocampal commissure, septum, etc., so that degeneration is widespread in many parts of the brain. Much of this is difficult to interpret and only the degeneration relevant to the commissural connexions of the basal rhinencephalon is reported.

In one specimen only the intertemporal limb of the anterior commissure is divided. The anterior limb is unaffected and shows no significant degeneration and there is none in the olfactory peduncles or bulbs. One may conclude that no fibres pass from the intertemporal to the anterior limb of the commissure.

In four specimens (178, 180, M10 and M14) the anterior commissure is completely divided close to the median plane. All show heavy degeneration in both limbs of the commissure, although a considerable number of normal fibres (estimated as about half the total) is still present. The degeneration in the anterior limb can be traced to the inner granular layers of both bulbs in all cases (Fig. 6). In one (M10) no degeneration can be traced further; in the other three an occasional fragmented fibre can be found in the external plexiform layer and among the periglomerular cells. The condition in the bulbs is practically identical with what is found in the contralateral bulb after unilateral lesions in the olfactory peduncle. It differs from what is found in the ipsilateral bulb after such lesions because of the relative lack of degeneration among the periglomerular cells.

Evidence for connexions from fibres of the anterior limb of the commissure in the anterior olfactory nucleus is less satisfactory. None is seen in one specimen (180) but in the other three a little degeneration debris among the cells of the nucleus (chiefly the rostral part and the pars externa) may indicate such connexions. They have been demonstrated in other mammals (e.g. by Lohman, 1963) and it is probable they are present in the coypu, but the present evidence is inconclusive. There is no evidence for connexions from the anterior limb of the commissure to any other parts of the brain.

DISCUSSION

From these experiments it may be concluded that in the coypu secondary fibres from the olfactory bulbs discharge to the anterior olfactory nucleus, the whole of the piriform cortex (the prepiriform and periamygdaloid cortices of Lohman (1963) but excluding the entorhinal or posterior piriform cortex), to the antero-lateral part of the olfactory tubercle, to the nucleus of the lateral olfactory tract, to the cortico-amygdaloid transition area in the amygdaloid fissure and, to a small extent, to the cortical amygdaloid nucleus. All these conclusions can be based on the first series of experiments in which the lesion is confined to an olfactory bulb, and the same experiments suggest very strongly that all fibres from the bulb run in the lateral olfactory tract, and that none enter the anterior limb of the anterior commissure or connect directly with the central amygdaloid nucleus or the bed nucleus of the stria terminalis.

So far as the amygdaloid connexions are concerned the negative findings are confirmed by the second series of experiments in some of which the olfactory peduncle is completely divided without causing any further degeneration in the amygdala. The other negative findings are less secure because none of the bulbar lesions is complete, but taken in conjunction with the similar findings of Cragg (1961), Lohman (1963), Powell & Cowan (1963) and Powell *et al.* (1965), there is little doubt that the lateral olfactory tract is the only projection pathway from the olfactory bulb and that its terminations are limited to the regions listed above. It is true that Cragg (1961) thought that some bulbar fibres entered the anterior limb of the commissure and discharged to the deeper cells of the piriform cortex and olfactory tubercle forming a deep olfactory projection pathway. This pathway undoubtedly exists, but as the work of Lohman (1963) and Powell *et al.* (1965) show, and also the observations recorded here, its fibres probably arise from the anterior olfactory nucleus and not from the bulb.

The secondary olfactory fibres terminate in an extensive cortical area on the base and lateral aspect of the brain limited rostrally by the circular sulcus which separates the bulb from the peduncle and laterally by the rhinal fissure. The terminology used for its subdivisions tends to emphasize, perhaps unduly, the cytoarchitectural differences within this area. Throughout there is an outer molecular layer. It is in this layer that the secondary olfactory fibres run and terminate, but it must be admitted that the Nauta technique demonstrates degeneration only up to the preterminal ramifications of fibres and not to the synaptic terminals themselves (Glees & Nauta, 1955; Bowsler, Brodal & Walberg, 1960). There is some doubt therefore if the presence of preterminal degeneration debris indicates endings in that precise situation, but at least they cannot be far away. Beneath the molecular layer lies a fairly well-defined lamina

of large cells, usually pyramidal in shape and often arranged in irregular clumps so as to give the lamina a corrugated appearance. Beneath this comes an ill-defined zone (it can hardly be called a lamina) of polymorphic cells. Cytoarchitectural differences do exist of course, and are not unimportant, but apart from the highly characteristic islets of Calleja in the olfactory tubercle they are not very striking and do not obscure the basic structural uniformity. The whole area forms an olfactory projection area, which, compared with the entorhinal area or the neocortex, is relatively simple in its cytoarchitecture. It is noteworthy that all the regions which can be differentiated within it, except the cortical amygdaloid nucleus which receives rather few fibres from the bulb, have retrogressed in an anosmatic mammal like the porpoise (Breathnach, 1953; Breathnach & Goldby, 1954). This is not the case with other parts of the so-called rhinencephalon. These vary in different mammals but the variations have no systematic relationship to the degree of development of the olfactory apparatus.

It has become clear also that the anterior limb of the anterior commissure is a complex system of fibres; it is certainly not a simple interbulbar commissure as Cajal (1911) thought. Most and probably all of its fibres arise from the anterior olfactory nucleus and it contains few if any which are commissural in the strict sense, that is, fibres which connect a part of one hemisphere with the same part in the other. Some are associational in character, probably connecting the anterior olfactory nucleus with the deep surface of the piriform cortex and olfactory tubercle (Cragg, 1961; Powell *et al.* 1965) and some cross to connect parts of the anterior olfactory nucleus with dissimilar parts of the same nucleus on the opposite side (Lohman, 1963). So far as the coypu alone is concerned, the evidence for both these sets of connexions is not as strong as for some of the other findings but suggests that the situation is similar to that found in the guinea-pig and rat. It is indeed probable that this fibre system is associational for all parts of the basal olfactory projection area although no connexions have been traced to more caudal structures such as the cortical amygdaloid nucleus, at least in the recent studies using the Nauta technique.

An important and now well established component of the anterior limb of the commissure consists of fine fibres to the olfactory bulb from the contralateral anterior olfactory nucleus, which end mainly in the inner granular layer. Other bulbo-petal fibres reach as far as the glomeruli or at least the periglomerular cells (they do not penetrate the glomeruli). As Cragg (1962) and Powell & Cowan (1963) and Powell *et al.* (1965) have shown, they are the fibres which degenerate in the deeper part of the lateral olfactory tract and come from the ipsilateral olfactory tubercle and possibly the rostral part of the piriform cortex. Lohman (1963) did not find them in the guinea-pig where the lateral olfactory tract appears to be entirely bulbo-fugal. They are present in the coypu, however. The authors cited have discussed the possibility that they exert a presynaptic inhibitory influence on the olfactory nerve terminals. The crossed fibres which reach the bulb from the opposite anterior olfactory nucleus must exert their influence mainly and perhaps exclusively in the granule cell layer.

SUMMARY

Lesions have been made in the brains of twenty-one specimens of *Myocastor coypus*, (i) in the olfactory bulbs, (ii) in the olfactory peduncles and anterior olfactory nuclei and (iii) in the anterior commissure close to the median plane. The resulting degeneration has been studied by the Nauta technique for frozen sections. The observations show:

(i) that all secondary fibres from the olfactory bulb run in the lateral olfactory tract and are limited in their distribution to the anterior olfactory nucleus, the piriform cortex, the antero-lateral part of the olfactory tubercle, the nucleus of the lateral olfactory tract, the cortico-amygdaloid transition area and the cortical amygdaloid nucleus. They all terminate superficially in the molecular layers in these regions.

(ii) the anterior limb of the anterior commissure receives no fibres directly from the olfactory bulbs. It consists of associational and decussating fibres from the anterior olfactory nucleus to the olfactory tubercle and piriform cortex of the same side and to the anterior olfactory nucleus and olfactory bulb of the opposite side. The fibres to the opposite bulb end mainly in the inner granular layer.

(iii) the lateral olfactory contains a few bulbo-petal fibres some and perhaps all of which end among the periglomerular cells of the olfactory bulb on the same side.

It is pointed out that these findings are very similar to those of Powell *et al.* (1965) in the rat and of Lohman (1963) in the guinea-pig, except that Lohman was unable to demonstrate the presence of bulbo-petal fibres in the lateral olfactory tract of the guinea pig.

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The results reported form part of a Ph.D. thesis (Makram Girgis, 1965) in which further details of the specimens and techniques are recorded. The thesis is stored in the University of London Library, Senate House, London, W.C. 1.

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